IV.—*Observations on Spiral Formations in the Cells of Plants.* By Dr. M. J. Schleiden, Professor of Botany in the University of Jena*.

[With a Plate.]

The first discoverer of spiral vessels, it matters not whether Henshaw, Malpighi, or Grew, was without doubt astonished in the highest degree by their elegant tissue; and the more he became acquainted with them, the more varied the forms unfolded before the eyes of the ingenious observer, the more eagerly attention must have been directed to this apparently so remarkable formation. Thence it happened that, although not agreed respecting the kind and manner, a higher import with regard to vegetable life was generally assigned to these parts in opposition to the cellular tissue.

It was soon, however, found necessary to place the annular and porous vessels by the side of the spiral vessels; and not relying on the observation of actual facts, but chiefly induced by their representative occurrence in similar or analogous parts, and misled by a false explanation of that actually observed, Link assumed the metamorphosis of these formations into one another, without, however, at the time expressing decidedly whether an ideal or real metamorphosis was intended. How far, then, this was from a correct comprehension of the matter, is shown by his subsequent writings and annexed illustrations, in which he still explained the fibres as the thinner places, and the elongated pores as remains of the thicker fibres, a view which he still entertained in 1831, with the greatest confidence, for the porous vessels. A view differing much from Link's, but quite as erroneous, was supported by Kieser; and even Meyen, in his 'Phytotomie,' declared the pores to be the remains of torn spiral fibre.

What, on the other hand, is at present understood by the word metamorphosis of the spiral vessels, has nothing in common with the earlier views, except the name retained for convenience sake; and by this alone Meyen seems to be misled, when in his Physiology (p. 139) he ascribes to Link the merit of having first decidedly advanced this doctrine. This is the more evident, as Link himself, in his latest edition of the 'Philosophia Botanica,' is still far from comprehending all the facts belonging to this subject, and comprising them under a correct point of view.

If we at present express the fundamental conception of this doctrine thus: "The thickening layers deposited on the

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primary simple cellular membrane have, on their first appearance, everywhere as a foundation an arrangement in a spiral band (or fibre) which becomes more or less distinct in various ways; and from this fundamental form are variously evolved all the numerous modifications of the so-called vascular and cellular walls, without, however, the one being to be regarded as a transitory stage of the other;"—then we must undoubtedly ascribe to Valentin (*Repertorium*, Part I.) the merit of having first advanced this doctrine in all its generality.

For along with those theories, observation had pursued her quiet course, and had found the porous and spiral formations in the cellular tissue also, and had gradually extended her discoveries so far, that at present it would perhaps be difficult, at least in the *Phanerogamia*, to point out any considerable masses of completely *developed* cellular tissue which do not manifest distinct traces of these textures.

I will here give a brief view of this doctrine from inquiries of my own, in which I lay claim to nothing new, more than those acquainted with the subject will ascribe to me; but, on the other hand, I dispense with the trouble of everywhere enumerating my authorities.

The cells of plants, including the so-called vessels, but with the exclusion of the laticiferous vessels*, the reducing of which to cells is still not at all clear to me, allow of two periods being distinguished in their life. In the first, that of their origin and isolated independent development, the membrane forming them grows, in its entire substance, by true intussusception. But as soon as the cells have adhered to form the cellular tissue and constitute the mass of a certain plant or its parts, this mode of growth either ceases entirely, or recedes so far into the background, that, from my observations up to the present time, I cannot venture to maintain its continuance; but neither can I deny it on account of the frequently very considerable expansion of the cells after the appearance of the succeeding formations. But in every case at present a new and by far predominant momentum is added, viz. that a new layer is deposited on the inner surface of the cellular wall, and indeed everywhere, in the form of one or more spiral closely wound bands, so that the coils, without continuity *inter se*, still mostly exhibit the completest contiguity. From personal observations, which, however, are still too imperfect to be detailed here, I think I may venture to conclude that originally there are always at

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least two such bands present*, whose extremities at the end of the cells pass into one another, and in most cases, even very early, cohere *inter se* to a single one.

Hence, then, proceed all the varied formations of the cells and vascular walls, according to the different influence of the following momenta.

A. The most essential circumstance, in my opinion, upon which is also founded the division of all these textures into two large principal groups, that of the Spiroidea (I borrow this expression, which is very useful, from Link), and that of the porous formations, is the following:

Either the cell has, at the time when the thickening of its wall by spiral deposition commences, already attained its complete expansion, or not.

I. Let us, in the first place, consider the latter case. Here, then, a second momentum becomes of importance; it is the cohesion both of the fibre and the cellular wall, and of the coils of the fibre *inter se*; at the same time, therefore, the number of fibres is likewise of value.

a. Simple fibre (double in the sense above stated). The cell still expands considerably from the instant of its origin; some convolutions cohere early, others tear asunder: *annular vessels* (of which a more detailed description below). In this case the fibre is generally not at all, or but loosely united with the cellular membrane.

b. Simple or compound fibre, a still rather considerable expansion of the cell, slight, or no cohesion with the cellular membrane: *spiral vessels with broad convolutions, capable of unrolling.*

c. Simple or compound fibre, extremely slight expansion of the cellular membrane, generally intimate cohesion with it: *narrowly wound spiral vessels capable of unrolling, false tracheæ,* and in part the *striped* and *scalariform vessels* of older writers.

d. Compound fibre, moderate expansion of the cell, cohesion in some places of the convolutions *inter se*, generally also with the cellular membrane: the whole series of the forms of the so-called *ramified spiral vessels* to the *reticulate.* Hereto likewise belong a portion of the *striped* and *scalariform vessels* of the older writers.

In these last, as well as in all the preceding, the law, *that the more intimately the fibre coheres with the cellular membrane, the less this can expand,* appears to obtain.

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II. But if the cell has, at the time when the spiral depositions have begun to form, already attained its complete expansion, a new and highly remarkable circumstance comes into action,—namely, that the formation of air-vesicles on the outer wall of the cell, between it and the adjacent ones, precedes the origin of the depositions; and the convolutions forming, closely lying one upon another, and in most cases rapidly cohering *inter se*, separate from one another cleft-wise at the place which internally corresponds to those air-vesicles. Since this process can be followed very far, and cannot, merely on account of the minuteness of the parts, be followed in several otherwise exactly similar formations, sound analogy advises us to extend it to all porous textures. This in general merely narrow slit, is often rounded by deposited formative substance, on which account the pore* appears the rounder the more the cell is developed; the longer, but more cleft-wise, the younger it is. Now to this division belong all *porous cells* and *vessels*, and likewise a portion of the earlier *striped* and *scalariform vessels*, which then only differ from those called porous by the length of the fissure of the pore.

B. A further momentum, which will here be but briefly noticed is, on the one hand, the form of the cell in the various intermediate stages between the two extremes of the small globular, and the much extended in length, in combination with an actual perforation of the primary membrane by absorption. To this head belong several formations, first indicated by Moldenhauer, and then correctly and fully described by Mohl, for instance, the leaf-cells of *Sphagnum*. But hereto more especially belong the difference between *cellular tissue* and so-called *vessels*, the latter being nothing more than cylindrical cells, generally situated in the same direction, with the terminal surfaces on one another, the septa of which are perforated in the most varied manner by absorption.

C. By far more important, however, is the following. Namely, in the vital process of the cell, spiral deposits are by no means at an end with the first layer; but they are repeated in many cases, almost as frequently as the volume of the cell permits. The rule then is, that the successive strata arrange themselves entirely according to the first, be this modified by the above-mentioned influences as it may, so that the places of the cellular wall not covered by the first deposit likewise remain free from all the succeeding ones. In this class is com-

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But we are now already acquainted with some interesting exceptions to this rule, namely, that after the first spiral deposit has been altered by the expansion of the cell, a new layer is deposited on the entire inner surface, on fibre and on primary cellular membrane without distinction; but since this second layer stands in a different relation to the primary cellular membrane from the first, it also must, according to what has been above stated, adopt a different form, viz. the porous. These formations of distant fibres, between whose convolutions pores are found, are exhibited, in fact, by a number of dicotyledonous ligneous cells, especially of such plants as are subject to the strong antagonism of the period of vegetation and of winter sleep. Thus, for instance, *Taxus baccata, Tilia europæa, Prunus Padus,* &c. An allied phænomenon is also found in the epidermis of the pericarp of *Helleborus fœtidus*.

The most important of these views I had already expressed in my memoir, "Contributions to our Knowledge of Phytogenesis," in 'Müller's Archiv. für Physiologie,' 1838*.

But recently have I been able to take in hand Mohl's "Memoir on the Structure of the Vegetable Cellular Membrane"†, (Tubingen, September, 1837); and I found, to my very great joy, that we entirely agree in two important points: first, in maintaining against Meyen, that every indication of a spiral, fibrous, or porous structure, is a certain proof that we have no longer to do with the original simple cellular membrane; and next, in his position: "Fibre and membrane differ merely by their size, and by the form in which they occur," which essentially agrees with my view that the spiral is only a secondary difference of form in the product of the vital force (in the fibre substance, or more correctly, the membrane substance). The slight chemical modification which I have demonstrated in it is, at least, far more inconsiderable, and consequently less essential, than the

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The most important of these views I had already expressed in my memoir, "Contributions to our Knowledge of Phytogenesis," in 'Müller's Archiv. für Physiologie,' 1838*.

But recently have I been able to take in hand Mohl's "Memoir on the Structure of the Vegetable Cellular Membrane"†, (Tubingen, September, 1837); and I found, to my very great joy, that we entirely agree in two important points: first, in maintaining against Meyen, that every indication of a spiral, fibrous, or porous structure, is a certain proof that we have no longer to do with the original simple cellular membrane; and next, in his position: "Fibre and membrane differ merely by their size, and by the form in which they occur," which essentially agrees with my view that the spiral is only a secondary difference of form in the product of the vital force (in the fibre substance, or more correctly, the membrane substance). The slight chemical modification which I have demonstrated in it is, at least, far more inconsiderable, and consequently less essential, than the

* Translated in Taylor's Scientific Memoirs, Part VI.

† The paper here alluded to, and Meyen's opinion on the same subject, have been placed before the English reader in Mr. Francis's translation of Meyen's Report on Vegetable Physiology for 1837.—Edit.

differences existing between the membrane of various plants and groups of plants *inter se*. Since Mohl and I have arrived at this result independently, and in part by a very different path, it is, in my opinion, a great presumption of its correctness. I gladly follow the steps of Mohl, whose memoir appeared some months earlier, as a confirmation only of a view already advanced; and would with joy always renounce in his favour all claim to priority, could I thereby for ever purchase an agreement of our convictions.

Scarcely more than in expression do Mohl and I differ in our views respecting the structure of the secondary deposits. If he admits an arrangement of the smallest parts in the direction of a spiral in the cases by far most frequent, and if I,—believing that I frequently have actually seen this arrangement even in cases where soon an apparent homogeneity occurs, and also as the changes produced by the expansion of the cells prove that the connexion of the molecules, in any other direction than that of the spiral, is in the younger stages almost nothing,—consider myself justified in speaking in all cases of a spiral striping or band, there is in this, with respect to the essential point, little discrepancy. I also believe that many differences of opinion, in subordinate points, will still disappear if Mohl keeps more accurately in view individual development, and especially pays more attention to the momentum of the expansion of the cells after the appearance of spiral deposits. Thus, for instance, in all my inquiries into the structure of the ligneous body, I have never contented myself with comparing the parts of different age of the same individual, but have constantly, as far as the material was at my disposal, at the same time pursued throughout a whole year the development of the same annular ring, by regularly repeated observations on the most varied parts of the plant. Highly instructive likewise is an accurate history of the development of the Spiroidea in the large Monocotyledonous vascular bundles, for instance, in *Arundo Donax*, where it must also be borne in mind not merely to compare on the same individual the younger with the older internodes, but to examine the homologous internodes on several individuals of different age. In this plant the spiroidea are situated in the perfectly developed fasciculus in a series radial from the axis to the periphery, arranged between the two large so-called porous vessels. The annular vessels, with the rings furthest from one another, are nearest to the axis of the internode, from thence towards the circumference the rings approach closer together, then pass

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into broad threaded spiral vessels, and these lastly into narrow threaded spiral vessels*. Now if the history of the development of such a fascicle be investigated, it is found that those distant ringed vessels were first formed as spiral vessels; that then, during the gradual expansion of the internode to which the vascular bundle belongs, the formation gradually progresses towards the exterior, and the last spiral vessel remains a narrow threaded one, merely because the longitudinal expansion of the cells was already nearly at an end when the spiral deposition took place. The two so-called porous vessels, on both sides, are, during the whole of this formative process, cylindrical cells, filled with a grumose fluid, and placed on one another, their walls being perfectly simple; and only after the expansion in length is terminated, the pores originate on their parietes in the manner described, frequently only in the direction of cells in the interior of the vascular bundle. At the same time the perforation also of the septa takes place, according to the law which seems to me pretty generally valid, that the horizontal septa, or those slightly deviating from this position, are only perforated with a round aperture, the steeper ascending ones become ladder-like or reticulate; and lastly, the steepest are merely provided with usual pores.

I conceive it arises from not paying due regard to this history of development that Mohl has not yet recognised the true origin of the annular vessels. I will, therefore, briefly communicate here what I have observed on this point.

All that Mohl has objected in another place against the erroneousness of the common view likewise supported by Meyen, that a tearing of the spirals into single coils, and a cohesion of the torn ends to rings takes place, remains perfectly correct; and I was long convinced of the untenability of that view before I had ascertained the true origin. The difficulties of actual observation of the process lie in what follows:—Of all spiroidea the annular vessels originate exactly from those cells in which a spiral deposition is earliest formed, therefore at a time when they are infinitely small and delicate. This period occurs in the outermost internodes of the bud, and every anatomist is aware of the almost insurmountable difficulties which here oppose a more accurate examination. It is true, the delicate indications of the spirals have undoubtedly been recognised everywhere here as of the earliest forma-

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tion; but instead of observing their development into rings, many have only inferred that the annular vessels were of far later origin. Moreover, the formation usually proceeds, at the moment when the bud comes to development, so rapidly, that the observation of the intermediate stages is rendered almost impossible by it. For obtaining a successful result everything here depends on finding a plant in which all these difficulties exist in a slighter degree, and on which therefore the process may be accurately observed; if once a clear insight has been acquired in this way, it is easy to find oneself at home, even with the more difficult plants. I found for these inquiries the *Campelia Zanonia*, Rich. (frequent in most hothouses), and the subterranean stem of *Equisetum arvense* most advantageous.

If the very youngest internodes of the buds of the first-mentioned plant be examined, a single extremely delicate and densely-wound spiral vessel is found in all the as yet scarcely limited vascular bundles. In older internodes the convolutions of this vessel are found further distant from one another, and near it exteriorly a new-formed narrow-threaded spiral vessel. But if we consider in this period the first formed vessel more accurately, Plate (fig. 11.), it will be seen that all convolutions are not separated in the same manner from one another, but that almost in regular alternation two entire coils adhere firmly together, and one convolution is drawn out. In still older internodes the extension is found to be so far advanced, that the free coil loosened from the cellular membrane frequently reaches as a mere band with a steep ascent from the one ring formed of two closed convolutions to the other. On still further developed vessels this elongated coil is seen corroded by the reabsorbing action of the cell, and all the stages of transition, as they are represented in the Plate (from fig. 1 to 5,) are frequently found in the continuity of a single vessel. Lastly, on still older vessels, the connecting coil is already perfectly dissolved; but there may still be observed on the isolated rings the extremities of the previous spiral fibre (fig. 6, 7, *a*.). Even on highly developed vessels, we still find on the perfectly closed and smoothened rings, their composition of two coils now and then indicated by single delicate dark lines (fig. 8—10.). Exactly the same process may likewise be easily followed in the subterranean stems of *Equisetum arvense*; and in particular we frequently find long streaks in vessels modified as is represented in fig. 11. as the first stage of transition to the formation of rings.

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sion of the three layers in the formations we meet with in the ligneous cells of *Taxus*, in the so-called vessels of the Lime, &c. Undoubtedly the primary simple cellular membrane here also constantly forms the outer layer, as to which I agree with Mohl, and no doubt can remain in the mind of the careful observer, that with regard to time the spiral fibres are earlier formed than the porous layer. But I am rather inclined to doubt Mohl's statement that this latter is developed between the primary cellular membrane and the spiral fibre layer. Mohl brings forward no reasons in support of it; and this whole hypothesis seems to me entirely unnecessary, and if only on that account to be rejected. There is no fact which requires such an admission for its explanation; but many, on the contrary, speak against it. Since the cellular membrane itself passes in forming, like all secondary depositions, in the same manner from a fluid through a semi-fluid state to a slighter or greater firmness, a period must necessarily occur in the process adopted by Mohl, during the origin of the porous layer, in which the spiral fibrous layer must be as good as entirely separated from the original cellular membrane, by the newly-formed still semi-fluid layer; or at least could be separated from it by the gentlest manipulation. But I have never been able to notice a trace of this in *Taxus*; and in *Tilia* exactly the contrary occurs, in so far as here in the cambial cells the spiral coils which then still lie densely together, are, it is true, to be unwound with difficulty; but as soon as the development of the cell begins, and long before the occurrence of pores, they are already firmly united with the membrane. The contrary likewise appears to me to result from an accurate investigation of the above-mentioned cells on the germen of *Helleborus fœtidus*.

Also with regard to the porous cells of the *Coniferæ*, I differ in some minor points from M. Mohl. It is true I concur in the main point with Mohl's exposition in refutation of Meyen's theory; but I must nevertheless confess that I think I have seen how in *Pinus sylvestris* the cells of the cambium, even in the latest annual rings, are constantly divided by delicate black lines into narrow spiral bands previous to the formation of pores, (as matter of course with perfect homogeneity of the primary cellular membrane,) and how these, which I regard as the boundaries of the adjacent convolutions, first disappear on the formation of pores; probably glued to one another in a similar manner as the cells themselves, whose boundary lines likewise frequently become invisible in more advanced age; for when I isolated the cells by boiling in caustic potash, even those from the outermost

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layers of the oldest heart wood constantly exhibited more or less distinctly these delicate stripes, and the pores then again appear merely as narrow clefts between two separating spiral coils.

In consequence of this view of mine of the constant generality of the spiral arrangement of the secondary depositions, I am also inclined, for the sake of consistency, to deduce the reticulated figures on the cells of the liber of the *Apocyneæ*, of the parenchymatous cells of numerous tropical *Orchideæ*, superposition *Dahlia* tubers, &c., rather from the adcumbency of two exceedingly delicate layers, formed of contrarily wound spirals, than to have recourse to quite a new mode of arrangement, which seems justified by no other peculiarity of the organ or of the occurrence. But I perceive it might be difficult here to bring direct observation in aid.

I may allow myself, in conclusion, some observations on the direction of the spiral coils. That all the reasons advanced by Meyen and Link respecting the difficulty of the determination do not at all affect the subject, is evident; for by reversion the relative position of two spirals is certainly not altered; but even the individual spirals remain wound right or left, in whatever way they are observed, of which Meyen may easily convince himself on a rod figured with a spiral. The being wound right or left of a spiral depends not merely on a different mode of viewing it, but on an internal difference in its mathematical construction. Moreover the sole actual difficulty mentioned by Mohl is not of such a nature that it cannot be overcome by a good microscope and some practice of the observer. In general I cannot agree with Mohl, that the spiral vessels principally occur wound to the right; I found some left-wound very frequently, and differences in various individuals of the same species. From my observations up to the present time, I have provisionally abstracted the following rule as at least very frequently valid. "In all spiral formations developing *cotemporaneously*, (comprising in the most general meaning all secondary depositions,) those which are situated *immediately* on one another in the direction of the radius are wound in the same direction; but those lying *immediately* on one another in the direction of the parallels to the periphery are wound in different directions. I will only mention here, as an instance, some spiroidea from *Cucurbita Pepo*; and I moreover appeal to the constant crossing of the pore fissures in contiguous parenchymatous and ligneous cells when observed on sections parallel to the medullary rays. But I must at once name, as a considerable exception, the peculiar short, thick, but delicate walled cells,

layers of the oldest heart wood constantly exhibited more or less distinctly these delicate stripes, and the pores then again appear merely as narrow clefts between two separating spiral coils.

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I may allow myself, in conclusion, some observations on the direction of the spiral coils. That all the reasons advanced by Meyen and Link respecting the difficulty of the determination do not at all affect the subject, is evident; for by reversion the relative position of two spirals is certainly not altered; but even the individual spirals remain wound right or left, in whatever way they are observed, of which Meyen may easily convince himself on a rod figured with a spiral. The being wound right or left of a spiral depends not merely on a different mode of viewing it, but on an internal difference in its mathematical construction. Moreover the sole actual difficulty mentioned by Mohl is not of such a nature that it cannot be overcome by a good microscope and some practice of the observer. In general I cannot agree with Mohl, that the spiral vessels principally occur wound to the right; I found some left-wound very frequently, and differences in various individuals of the same species. From my observations up to the present time, I have provisionally abstracted the following rule as at least very frequently valid. "In all spiral formations developing *cotemporaneously*, (comprising in the most general meaning all secondary depositions,) those which are situated *immediately* on one another in the direction of the radius are wound in the same direction; but those lying *immediately* on one another in the direction of the parallels to the periphery are wound in different directions. I will only mention here, as an instance, some spiroidea from *Cucurbita Pepo*; and I moreover appeal to the constant crossing of the pore fissures in contiguous parenchymatous and ligneous cells when observed on sections parallel to the medullary rays. But I must at once name, as a considerable exception, the peculiar short, thick, but delicate walled cells,

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which in their interior contain plate-like rings and spirals raised on the narrow edge, which constitute nearly the entire mass of the wood of the *Mammillariæ, Echinocacti,* and *Melocacti;* and also occur in small quantity in the *Opuntiæ,* especially at the contractions of the joints, and which were first described by Meyen from *Opuntia cylindrica.*

EXPLANATION OF PLATE.

Fig. 1—10. Stages of the formation of the annular vessels from *Campelia Zanonia,* Rich. Explanation in text, page 42.
Fig. 11. Commencement of the formation into a ring of a spiral from *Equisetum arvense.*
Fig. 12. Spiroidea on a section through the medulla perpendicular to the bark; *a.* the side towards the medulla, *b.* that toward the bark.
Fig. 13. Spiroidea on a section parallel to the bark.
Fig. 14. The same as in fig. 13, with an intermediate series of cells corresponding to a right wound spiral.
Fig. 12—14. From young stems of *Cucurbita Pepo.*

V.—*Characters of new Genera and Species of New Holland* Cyperaceæ, Restiaceæ, and Juncaceæ. By Prof. C. G. Nees von Esenbeck.

[*Communicated by Professor Lindley.*]

A. Gunnianæ.

Helothrix.

Locus inter Cyperaceas Acrolepideas.

Gen. Char. Spicula disticha, squamis duabus inferioribus minoribus sterilibus, duabus superioribus hermaphroditis. Stamina tria. Perigynii setæ 4 (an semper?) retrorsum scabræ. Stylus bifidus, a basi bulbosa deciduus. Caryopsis biconvexa, styli basi conica mucronata perigynioque stipata.

Inflorescentia: spiculæ axillares et terminales geminæ brevipedunculatæ.

Plantæ pusillæ habitu *Acrolepidis,* Schrad. aut *Eleogitonis,* in inundatis degentes, diffusæ. Culmus ramosus, flexuosus, foliosus.

*974. *Helothrix pusilla.* Culmi 2—4 poll. longi, flaccidi, geniculati, compressi. Vaginæ internodiis breviores, totæ herbaceæ, striatæ ore truncatæ. Folia linearia, angusta, obtusa, margine scabra, trinervia. Spiculæ vix lin. 1. longæ ex vaginis superioribus emergentes, pleræque geminæ, pedunculis inclusis, oblongæ, compressæ, virides cum purpura. Squamæ carinatæ, duæ inferiores triplo majores uninerves acutæ, duæ superiores ovato-lanceolatæ obtusæ trinerves, apice virides, basi pallidæ, deciduæ. Stylus bifidus, ramis longis tortis hirtis. Caryopsis candida,

* The numbers refer to the collections of dried plants given away by Mr. Gunn.

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